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OUR NORTH-AMERICAN ECHIURIDS.

A CONTRIBUTION TO THE HABITS AND GEOGRAPHICAL RANGE OF THE GROUP.

CHAS. B. WILSON.

ONLY four species of Echiurids, representing three of the five known genera, have been reported from the North American coast up to the present time. These are as follows: *Thalassema mellita* Conn was found at Beaufort, Va., living in empty sand-dollar tests, and its structure and morphology were most admirably worked out (2). *Thalassema viridis* Verrill has been reported from nodules of blue clay at a depth of seventy-seven fathoms off Head Harbor, Campobello Island (16). *Bonellia sühmii* Selenka was dredged from deep water off the coast of Nova Scotia and was described and named in the *Challenger Reports* (12).

The fourth species, *Echiurus chrysacanthophorus* Pourtales, has been reported by several authors from various localities on the New England coast. Each of these four was established as a new species by its discoverer and has been found nowhere else. The Bonellia species was based upon a single badly mutilated specimen, *T. viridis*, and the species of Echiurus upon a very limited number of specimens, no one of which in the latter species was perfect, leaving *T. mellita* to stand alone beside the well-known and thoroughly studied European forms.

In the present contribution I am able to add American localities for two of the well-known Old World species, and when

the results of the recent Harriman Alaskan Expedition are published another even better known European form will be found among them.

It is hoped also to clear up the cloud of doubt which has hung about the questionable American *Echiurus chrysacanthophorus*, for the reports on this species have contained so many gross errors and conflicting statements, and so little accurate description, that the determination of the exact species has been impossible.

This has been due to a variety of causes, chief among which may be mentioned two. First, it is essentially a shore species, frequenting muddy shallows where the water is too deep or too roily for the shore collector and not deep enough for dredging. Consequently only a limited number of specimens have been obtained.

Again, so far as known, every one of these was so mutilated in the getting as to render a full description impossible. The part most easily injured is the delicate proboscis. This breaks off upon the slightest provocation, and leaves no scar that can be detected even with a good hand lens.

Hence it is difficult to obtain a specimen with the proboscis intact even under favorable circumstances, and absolutely impossible by dredging. It was this denudition of the proboscis with no resultant scar which led the discoverer of the species, Couthouy, to mistake it for a holothurian, and to describe it as *Holothuria chrysacanthophora* in 1838 (3).

The same mistake was made by Gould in 1841 (5), who says: "This is not unlikely to be *H. forcipata* of Fabricius. Several specimens which I have seen were all taken from fishes' stomachs in a mutilated state. Some of the essential characters, therefore, remain yet undetermined. The surface is light colored and appears to be naked, except that there are several long, flexible, sharp-pointed spines about the mouth[1] of a shining golden yellow. One specimen is five or six inches in length."

Pourtales rectified this mistake in 1851 and located it correctly among the Gephyrea, giving it a name which it has since

[1] Really the anus.

borne, *Echiurus chrysacanthophorus* (8). But he also adds: "I have seen but a single specimen of this species. The one I have before me answers very well to the characters assigned to *Echiurus Gaërtneri* by Quatrefages. It wants likewise the spoon-shaped appendage," *i.e.*, the proboscis (*ibid.*).

But Quatrefages himself admitted in 1865 that the species Gaërtneri was based "upon individuals which had been rolled about by the wind," and he adds: "It is very possible that the appendage was broken off" (10). This proved to have been the case, and in 1880 Greef included the species Gaërtneri as one of the synonyms of *E. Pallasii* Guerin, but he retained the doubtful species chrysacanthophorus (7).

A species of Echiurus has been dredged by Professor Verrill at various points along the New England coast, and has been reported conditionally as *E. chrysacanthophorus*. But Verrill wrote me in 1895 that in all his dredging (over 1000 localities) he had met with this species "in very few instances, and *never*[1] a perfect specimen." Hence he wisely refrained from attempting any detailed description of it, and from any comparison with foreign species.

Finally Shipley, in 1896 (13), and again in 1899 (14), rejects the species altogether as being inadequately described, and the locality, "North Atlantic," which he assigns to *Echiurus Pallasii*, doubtless signifies the Norwegian and Greenland shores, from which it has been reported by other authors.

Such being the condition of affairs, it seems fitting to describe the species accurately, to determine it definitely, and to add a few observations upon its habits which may be of generic interest. This is rendered possible by the fact that it has been the good fortune of the author to obtain a large number of absolutely perfect specimens and to keep some of them under observation in aquaria for several weeks, while others were successfully preserved, — a by no means easy task.

The material was all obtained at Casco Bay, on the Maine coast, during the summers of 1895–98. It is also hoped that the photographs which accompany these notes may prove of assistance in locating the species.

[1] The underscoring is his.

Habits. — This species lives in the mud near and below ordinary low-water mark. It can be best obtained during the few days of each month when the tides run lowest, at which time it can be dug in the same way as the common clam (mya).

It is most abundant in close proximity to mussel beds where the mud is soft and very black with organic matter.

I am aware that this habitat is radically different from that given by Greef and others for *E. Pallasii*, but I find a ready explanation in the fact that sand beaches are the rare exception rather than the rule along the Maine coast, so that the animal has simply accommodated itself to its environment.

Its home is a simple burrow formed by pushing aside the mud. The manner in which this is done was repeatedly observed both in its native haunts and in an aquarium.

If not already in that position, the animal turns until it rests upon its ventral surface. This brings the two large anterior setae in contact with the mud. The proboscis is now turned upward and backward, until it lies along the dorsal surface of the body, with its own ventral surface outermost, but protected somewhat by a rolling in of its edges. The proboscis remains inert in this position and *takes no part whatever in the burrowing*. This is in strong contrast to the active locomotor use of the proboscis described by Rietsch in a specimen of *Bonellia minor* (11). By a series of muscular contractions, which include both the longitudinal and circular muscles of the body walls and the special muscles which move the ventral setae, these latter are thrust forward until they project in front of the body almost horizontally.

At the same time the base of the proboscis is drawn backward and somewhat upward, so that the anterior end of the body becomes wedge or chisel shaped, the ventral surface being flattened and extending farthest forward, with the two setae projecting from its anterior edge. These setae are then turned downward and thrust into the mud as far as possible. Being curved, they furnish an excellent leverage, and the body is drawn toward them by a contraction of the longitudinal muscles.

This contraction passes slowly backward along the body until the posterior end is reached, which is moved forward

thereby half or three-quarters of an inch. The two anal rows of setae now serve to hold it in position, while the anterior end is again thrust forward and downward into the mud, and the ventral setae are fastened in a new position. This process is repeated until the animal finally disappears beneath the surface, leaving a circular opening equal in diameter to the body at its greatest lateral contraction. The whole process is extremely slow, and fully forty minutes are consumed in getting the posterior end of the body out of sight beneath the surface.

The burrow proceeds diagonally downward for ten to eighteen inches, then runs horizontally from six inches to two or three feet, and finally turns vertically upward again toward the surface.

When the animal reaches the surface the anterior end of the body is pushed out far enough to free the proboscis. This is then restored to its normal position and the body is withdrawn again into the burrow.

Spengel notes (15) that each burrow of the species (*E. Pallasii*) observed by him at Nordenay possessed two openings close together and each surrounded by a low wall. But those burrows were made in hard sand, while these are in soft mud, and consequently we should expect to find differences. These burrows at first have two openings, but the original entrance soon fills up through the caving in of its walls and the washing in of mud from the surface. The entire diagonal portion is often filled in this way and is never opened again, leaving this end of the burrow blind. These burrows also, when first formed, have low walls around the openings, caused by the pushing aside of the mud, but they quickly disappear.

The Echiurus assumes a position just below the surface, holding itself in place by the two rows of anal bristles (*cf.* Shipley). The mud then washes into the burrow and forms a plug one to two inches thick, with a small opening about the size of a lead-pencil at the center. Through this opening the proboscis is thrust out in search of food when the tide is in, and is then the only portion of the animal which is visible. It is capable of great extension, as was the proboscis of *B. viridis* described by Eisig, and often reaches a length of five or six inches. The

free end moves about in every direction and carefully searches the surface around the opening. Having found a particle of food, the edges are rolled in ventrally toward each other, if not already in that position, and form a more or less closed tube. The whole ventral surface (which is now the interior of the tube) being ciliated, there is generated a current which quickly carries the food toward the mouth. The proboscis often assumes a similar tubular shape when it is not elongated, as can be seen in Fig. 2, so that the curling inward of the edges is independent of the strong contraction of the circular muscles which produces the extension.

Often also it rolls itself into a tight coil, commencing at the tip and curling over ventrally as though it were grasping some object, but nothing save a few food particles is to be found in it, which are much too small to occasion any such effort.

The proboscis is very sensitive over its entire surface, but especially so on the ciliated ventral portion, and the slightest irritation there results in a quick withdrawal.

As would be inferred, such an appendage is of extreme importance to the animal, and yet it breaks off upon the slightest provocation. Whether such a separation is necessarily fatal or not, and whether the animal possesses the power of regenerating its proboscis, could not be definitely determined.

It hardly seems probable, however, that the animal could live for any length of time without it. But it was found that the proboscis itself was so highly innervated that it retained its vitality, and to a marked degree its sensitiveness also, for a long time after separation, a week or more if kept in fresh sea water. When the tide goes out, though there is always water left in the burrow, the proboscis is withdrawn and all indications point to the conclusion that the animal retreats to the lower part of its burrow.

Like other gephyreans, this species secretes a thick mucus, which lines the burrow walls and penetrates the mud for some distance, giving it greater firmness and solidity.

This mucus, as in so many other cases, oxidizes the iron in the mud, so that the walls of the burrow are a rusty brown color and stand out in sharp contrast to the surrounding black.

Movements and Locomotion. — In life, even when out of its burrow, the creature is constantly altering its outward form by energetic contractions of the skin muscles, as noted by Greef (6). Deep constrictions appear at various places, which move now forward, now backward, that portion of the body just in front of or behind the constriction increasing proportionately in size. The proboscis is also kept in constant motion, coiling up and uncoiling, rolling inward from the edges and unrolling or stretching out to a considerable distance and then being withdrawn. In its burrow the animal cannot turn around, but can move either forward or backward at will and with equal rapidity. This motion is accomplished by a series of wave-like contractions and relaxations in the circular and longitudinal muscles of the body wall, the one alternating with the other, and both together producing a fairly rapid gliding motion. The necessary rigidity is given to that portion of the body wall which for the time being serves as a fulcrum, by the pressure of the liquid in the body cavity, as first noted by Quatrefages (9). Andrews has clearly stated (1) the essential factors in the mechanism of *Sipunculus Gouldii* which bring about such "hydrostatic locomotion," and several authors have described similar motion in other gephyreans.

But no one, so far as known, has suggested any other mode of moving about. Indeed, one of the best recent text-books distinctly states that "the gephyrea are only capable of a very slow creeping motion" (Parker and Haswell, p. 461).

It seems never to have been suggested to any one, the present author included, that this same rhythmic contraction of the body walls would furnish an excellent means for swimming.

Hence it was quite a surprise, on visiting an aquarium after dark during the second summer, to find three or four specimens swimming about in it freely. The body was elongated to twice its ordinary length, while the proboscis was elongated even more in proportion and its edges were rolled downward and inward so as nearly to meet along the median line and form a long narrow tube which seemed to take an active part in the swimming.

The resultant motion was peculiar, being gyratory or cork-

screw-like, the anterior end always moving ahead, but it was perfectly free in any direction and quite rapid.

Besides assisting in locomotion the proboscis also seemed to serve as a steering organ, and its extreme sensitiveness rendered it very effective in avoiding obstacles.

The fact that this swimming took place only at night suggests that these animals are more or less nocturnal in their habits, and it may be that they can move about much more freely than has been hitherto supposed. At all events this is probably the mode of locomotion used at or near the breeding season, and it readily explains the large numbers of specimens which are thrown up on the beach after a storm at such seasons.

This species is well known to the clam-diggers along the coast and is sometimes used for bait in deep-sea fishing, but not often, and is never sought designedly for that purpose.

Determination of Species. — After a careful comparison of the descriptions given by Couthouy and Pourtales with that of *E. Pallasii* by its discoverer and subsequent zoölogists, and with the description which follows, there seems no possible doubt that those authors fell into the same error concerning our American species which trapped Quatrefages on the European form, *viz.*, they described an *Echiurus Pallasii* which had lost its proboscis as a new species. Accordingly *Holothuria chrysacanthophora* Couthouy, 1838, and *Echiurus chrysacanthophorus* Pourtales, 1851, must go to swell the long list of synonyms already appended to *Echiurus Pallasii* Guérin-Méneville.

Echiurus Pallasii Guérin-Méneville. — Synonyms: *Holothuria chrysacanthophora* Couthouy, 1838. *Echiurus chrysacanthophorus* Pourtales, 1851.

External Morphology. — Body like that of all known echiuroids, spindle-shaped, tapering slightly at either end; 10–30 cm.[1] long (including the proboscis, 3–6 cm. long) and 3–6 cm. in diameter at the center (Figs. 1 and 2).

[1] This figure is much larger than that usually given for *E. Pallasii*, but is the result of careful measurement and is good evidence in favor of Shipley's statement (13). "It seems probable that *E. forcipatus* of Reinhardt is identical with *E. Pallasii*, though bigger" (*cf.* p. 175).

Color uniform gray or grayish-yellow, shading into a deep orange on the interior of the proboscis. Entire surface of the body rough from being covered with small blunt papillae, which are unequal in size. The larger ones are more globular and are quite regularly arranged in transverse rows in which the individual papillae are so close together that they touch one another. There are twenty-two or twenty-three of these rows, and between them are scattered the smaller papillae, which are more conical in shape and seldom show any arrangement in rows.

Both kinds of papillae are more sharply defined and nearer together toward the ends of the body. There is also usually a bunching of the papillae around the anterior setae where they are larger than elsewhere on the body.

There is a pair of large, shining yellow, hooked setae, one on either side of the ventral mid-line, 16–20 mm. behind the base of the proboscis. These setae are about 20 mm. long and curve toward the posterior end of the body. They are retractile and can be almost wholly withdrawn into the body cavity. The posterior end of the body is surrounded by two rows of yellow setae, somewhat shorter than the anterior pair and perfectly straight. They also are retractile, and in most preserved specimens are withdrawn into the body cavity. In the animal shown in Fig. 4, however, they were extended to their full length. The rows are quite near together (3–5 mm.) and not more than 4 mm. from the anus, which is central and terminal. These posterior setae incline backward and assist the animal in moving about. The anterior row is made up of eight or nine setae, the posterior one of seven or eight.[1]

Reserve setae are present for both rows and for the ventral pair. The setae alternate in the two rows, but neither row is entire, a space being left on the ventral mid-line.

In the posterior row this space corresponds to the omission of one seta, in the anterior row to the omission of three.

There is a papilla around the base of each seta, much larger than those on the body. The spaces between these basal papil-

[1] The fact that these different numbers may be found in individuals otherwise exactly alike is still further evidence that Reinhardt's species, forcipatus, is not well grounded.

lae and the intervals on the ventral surface, up to within 1 mm. of the mid-line, are filled in with ordinary large papillae.

Proboscis large, 3–6 cm. long and 1–3 cm. wide. It is capable of being extended to 12 cm. with a corresponding diminution of its width. It is cylindrical at the base, but quickly opens into a half tube which is broadened at the tip into a shovel form (Fig. 1). The exterior is a brighter yellow than the body and perfectly smooth. The interior is rich orange and completely ciliated, but in most specimens examined it lacks the longitudinal brown stripes noted by Greef in *E. Pallasii* (6). In several specimens, however, they showed up faintly against the orange background.

The skin also on the interior of the proboscis is thrown up into longitudinal ridges, the intervening furrows between which are darker in color than the ridges themselves (Fig. 3). The mouth opens through the center of the cylindrical base. A well-defined ridge runs outward from the mouth along the dorsal mid-line toward the tip of the proboscis. This ridge is somewhat brighter in color than the rest of the interior, but is completely concealed unless the proboscis is opened. The tip of the proboscis sometimes has a well-marked chocolate-brown edge.

The ventral nerve cord and blood vessel show plainly through the skin (*cf.* Figs. 1 and 2), and when the body is extended the dark-colored intestine can be seen at points where it touches the inner surface of the body walls. The sexes are alike externally, with no appreciable difference in size (*cf.* Figs. 1 and 2).

But when sexually ripe, Greef says that the golden eggs or the white semen in the nephridia show through the body wall enough to distinguish the males from the females (6).

Internal Morphology like that of all echiuroids. The alimentary canal is several times the length of the body and is looped irregularly. It is suspended from the body walls by thin muscular strands instead of a continuous mesentery, and upon the slightest perforation of the body walls it is extruded through the orifice by a violent contraction of the muscles.

This alimentary canal may be divided into three regions or parts, called respectively the fore, mid, and hind gut.

The foregut is very short, and contains a pharynx and oesophagus which are often bright orange in color like the inside of the proboscis. The remainder of the foregut is usually larger in diameter and has been called the crop. The midgut constitutes the bulk of the alimentary canal and is distinguished by a groove lined with vibratile cilia which runs along its dorsal side. Opening into this groove at either end is a collateral intestine, much smaller in diameter than the midgut and seemingly analogous to that in echinoderms.

The hindgut is somewhat larger than the midgut and forms near the anus a cloaca into which open two anal vesicles, one on either side. These are quite long, simple sacs, light brown in color, which vary greatly in length in different individuals (40–70 mm.). They open into the body cavity by ciliated funnels, which are most numerous near the base of the sacs, and one of which is terminal.

Both males and females have two pairs of nephridia, which open on the ventral surface on either side of and close to the nerve cord. The mouths of these nephridia are raised into large papillae on the external surface of the body, and can be plainly seen, the anterior pair just behind the ventral setae, and the second pair 5 or 6 mm. farther back.

At the base of each nephridium on the inner side is a ciliated funnel opening into the body cavity, through which the sexual products enter the nephridium when sufficiently ripe.

They are then discharged through the external papillae into the water. When free from eggs the nephridia are 15–20 mm. long and spindle-shaped, with a diameter of 3–5 mm. at the center. Probably when filled with ripe eggs or sperm they increase proportionately in size.

The *Sexual Products* are doubtless formed, as stated by Greef, from small cells near the posterior end of the ventral nerve cord, which are covered with peritoneum. But reproduction certainly does not take place in this locality (Casco Bay) in July and August, as well as in midwinter, *viz.*, it does not occur twice a year. All my specimens were secured in June to August, and not one of them contained ripe sperms or eggs.

But two specimens were obtained September 4 and placed in an aquarium. One of these, which proved to be a female, was injured in the digging, and while being put into the aquarium some nearly ripe eggs escaped through the rent in her side. These furnished the necessary stimulus for the uninjured male and he soon sent out ripe sperms in large quantity from the nephridia.

This would indicate a breeding season for that locality of September to November.

In the female just mentioned the nephridia were perhaps one-eighth full of eggs; all the rest of the eggs were free in the body cavity. This was the only specimen in which any eggs were found in the nephridia, but they may sometimes be found in the body cavity in June, and probably require a long time for development. When ripe (*i.e.*, those from the receptacles) the eggs are spherical, about 0.3 mm. in diameter and nearly opaque, but until fertilization the large germ nucleus can be plainly seen through the yolk granules.

The spermatozoa have a peculiar bullet-shaped head, a short cylindrical middle piece, and a long, very delicate tail. Their vibratory movements are rapid and very strong, and they retain the power of motion for a long time after being discharged into the water.

Just enough description has been here given to fix the species definitely, but considerable work has already been done on the morphology and histology of the body organs and on the origin of the sexual products, and it is expected that the near future will afford an opportunity for a careful study of the complete life history of this interesting species.

Through the courtesy of Dr. W. R. Coe, of the Sheffield Biological Laboratory at Yale University, I have received specimens of an Echiurus secured by him in Alaska, while on the Harriman Alaskan Expedition during the summer of 1899.

This species was found abundantly at many different localities along the Alaskan coast south of the Peninsula and on adjacent islands, nearly always in rich black mud.

It is of considerable interest to note that it proves to be the same species here described, *viz.*, *Echiurus Pallasii*, and that

its habits, so far as observed, correspond exactly with those just given. Its burrow is horseshoe-shaped, the two ends opening at the surface, and around each is a little mound formed by the pushing aside of the mud. The iron ingredients of the mud in the walls of the burrow are also discolored by the mucus secreted by the animal and show as a rusty brown.

In size the Alaskan specimens surpass those from Casco Bay, and the same shovelful of mud often reveals giants and pigmies of the species side by side. But this is simply in accordance with the general results of the expedition, for gigantic specimens of nearly every native species were found.

The number of setae in the anal rings of four specimens selected at random were counted. In three of these there were eight setae in the anterior ring and seven in the posterior, but in the fourth specimen the numbers were nine and eight respectively.

The fact that specimens from two such widely separated localities agree perfectly in carrying the maximum of size beyond 30 cm. and also in the variation of the number of setae in the anal rings, is a third argument, and quite a strong one, against the validity of the species forcipatus.

There seems to be no discernible connection between the number of the setae in the anal rings and the size of the animal; a small specimen is just as likely to possess the larger number.

On the contrary, there is something of a connection between the size of the individual and the temperature of its environment; in general, the colder the water the larger the average of the species. Such a fact strongly corroborates the statement made by Shipley (14) that "this genus is a denizen of the colder seas," and indicates that an Arctic environment is most congenial to its development.

These two new localities also go far toward rendering this species cosmopolitan. It has already been reported from the North Sea, where it was originally discovered, the English Channel, and the coasts of Norway, Sweden, Denmark, Holland, and Belgium. To these can now be added the American North Atlantic and North Pacific, and it may be expected as

one of the results of further investigation in the Asiatic North Pacific.

Thalassema erythrogrammon Max Müller. — I obtained a specimen of this Thalassema through the kindness of Dr. E. A. Andrews of Johns Hopkins University.

It was taken at Green Turtle Cay, off Great Abaco Island, the Bahamas, in the summer of 1886, and when alive was of a flesh color with reddish longitudinal stripes, the proboscis lighter in color, the papillae whitish. The body was raised into longitudinal ridges between the muscle bundles whose prominence varied with the degree of contraction. The specimen was hardened in Perenyi's fluid, and yet the muscle bands show a decided pink-brown color at the present time and stand out very distinctly, as can be seen in the photograph (Fig. 5).

It was excellently preserved in a normal condition and measures 16 cm. in length (including the proboscis, 3 cm. long) and 2.4 cm. in greatest diameter. Body spindle-shaped, with bluntly rounded ends, and after preservation *not* perceptibly furrowed by the longitudinal muscle bands. Papillae in dense placques at the posterior end of the body; no smooth area in the immediate vicinity of the anus. Longitudinal muscles in sixteen bands about 1.5 mm. wide, with interspaces 4.5–7 mm. wide at the center of the body, except the two bands on either side of the ventral mid-line which are close together.

Proboscis so fleshy as to be nearly a solid cylinder, 1 cm. in diameter at the base, thus bringing the mouth to the extreme ventral surface; less fleshy and not broadened toward the tip.

The two setae were so far withdrawn into the thick skin as to be wholly invisible from the external surface, but could be all the more plainly seen on the interior.

The specimen proved to be a ripe male, and the three pairs of nephridia were enormously swollen and packed with sperm.

They increased in size from in front backward, the respective lengths being 3.2, 4.5, and 8.2 cm. The two posterior pairs were constricted at intervals and looked much like a string of sausages; the anterior pair opened 3 mm. in front of the ventral setae, and all three pairs were furnished with spirally coiled internal openings.

Anal glands 9 cm. long, simple, very thin walled, and *without* visible funnels. Intestine filled with the powdered shells of small lamellibranchs.

The chief interest in this specimen centers in the new locality. It has been reported hitherto only from the Red Sea, the Isle of Bourbon, the Malay Peninsula, and New Guinea, about as far distant as possible from the Bahamas. But it evidently belongs to the West Indian fauna and adds one more to the Atlantic species of this genus. Again, this is one of the species in which the number of muscle bands has been given as invariable and fourteen in number. The occurrence of sixteen bands in the present specimen shows that, like most of the other species, the number varies within narrow limits. The position of the anterior nephridia in front of the anal setae, as in *T. caudex* Lampert, is also worthy of note.

STATE NORMAL SCHOOL,
WESTFIELD, MASS.,
March 8, 1900.

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FIG. 1. — A male (right) and female (left) *E. Pallasii* in a normal state of contraction in sea-water. × ½. Photographed from life.

FIG. 2. — The same pair in the same position, but with the female contracted under irritation. × ½. Photographed from life

FIG. 3.— Ventral view of proboscis and anterior body. Photographed from preserved Alaskan specimen. Life size.

FIG. 4.— Anal rows of setae. Photographed from preserved specimen. Life size.

FIG. 5.—*Thalassema erythrogrammon*. Photographed from preserved specimen. ⅔ actual size.

SOME GENERAL FEATURES OF THE METAMORPHOSIS OF THE FLAG WEEVIL MONONYCHUS VULPECULUS FABR.

JAMES G. NEEDHAM.

I HAVE been for some time desirous of studying the development of some beetle which would represent metamorphosis in as complete a condition as is found within the order Coleoptera. Last summer I found an abundance of the flag weevil (*Mononychus vulpeculus* Fabr.) in all stages; and this furnished me the opportunity for which I waited. The larvae of this beetle are little fat grubs, which eat the seeds of the blue flag (*Iris versicolor* Linn.). They are sheltered from first to last within the flag capsule and are very degenerate. They lack eyes, antennae, and legs, as well as wings. They represent a sort of ecological specialization, common among the higher insects, manifest in the adaptation of life to very special situations, and of life history to conditions of transient food supply.

I. *Life History.*

The life history of this long familiar species seems not to have been fully made known.[1] While gathering my material I was not seeking to determine the full life history, but now I find that my collections and notes reveal it pretty completely. Collected material gathered in at intervals of two or three days give data as follows: Eggs were first found June 8. The beetles had just begun to oviposit on the earliest of the flag flowers, first opened that day. Larvae were first found June 29, at which

[1] Dr. John Hamilton published fragmentary notes on its life history in 1894 ("Mononychus vulpeculus and its Parasites," *Entom. News*, vol. v, pp. 287, 288), describing oviposition and the form and feeding habits of the larva, and citing an instance of great destructiveness on the part of two parasites, *Pimpla inquisitor* Say and *P. pterelas* Say.

time but few eggs were hatched. Pupae were first found August 5, and newly transformed imagoes, August 8, two months after egg-laying began.

Examining my collection of several hundred larvae, after the manner of lepidopterists, I find among them three sizes of head, so distinct as to certainly indicate three larval stages. The first, which is of the size attained before hatching, measures in diameter .24–.26 mm., the second .40–.44 mm., and the third .81–.85 mm.

My notes and collection labels together indicate the following life history:

1. An egg stage, lasting about three weeks. The eggs lie at the bottom of punctures made through the wall of the flag ovary by the mother-beetle with her rostrum. The egg is pellucid white, broadly oblong-oval in outline, and measures .38 by .70 mm.

2. A first larval stage, lasting about five days. At the end of this stage an average larva measures 2.2 mm. in length by .4 mm. in greatest diameter.

3. A second larval stage, lasting perhaps ten days (certainly not over two weeks), at the end of which the larva measures 4.60 mm. in length by 1.02 mm. in greatest diameter. Thus far the larva remains slender and quite elongate. During these two stages it traverses the outer face of from three to five seeds, leaving a slowly widening, shallow, brown furrow across their surfaces.

4. A third larval stage, lasting a very little more than two weeks, and divided into two periods:

(*a*) A period of feeding, and extraordinarily rapid growth, lasting hardly more than a week. The greater part of increase in size is attained during this short period. During it the larva is boring through the center of several seeds, feeding on their highly nutritive endosperm. At the end of it the larva measures 6.5 mm. by 2.5 mm.

(*b*) A period of transformation to the pupa.

5. A pupal stage, lasting, apparently, not more than a week, spent within the larval burrow. The pupa is naked and smooth, except for a pair of recurved spines on the tip of the abdomen.

6. A period of adult life, lasting ten or more months. Of this time a month or more is spent (lasting until the bursting of the

flag capsules in autumn) quietly within the larval burrow; eight or more months are spent in hiding in winter quarters; activity only begins with the season of iris flowering, and lasts for about a month. Oviposition continues sparingly after the first week. Except at the beginning of the season, several developmental stages may be taken at the same time, and this fact renders dates of *first observation only* of value as indices of life history.

The more striking features of this life history are:

1. The small number of larval stages, for a representative of this order.[1]

2. The exceedingly rapid growth during the first period of the third larval stage. That an animal which will live a year should attain the greater part of its growth within a week is indeed a striking phenomenon. To be sure, this growth is mainly increase of fat.

3. The long period of adult inactivity, extending through two stretches of warm weather.

The metamorphosis of this beetle is very complete. The segregation of the development life into growth period (period of partial anabolism — fat-making) and differentiation period is very marked. The transformation of the degenerate larva, lacking wings, legs, antennae, eyes, optic lobes, and salivary glands, into the adult with all these parts well developed, is very rapid. There are excellent reasons for believing that these things have been independently acquired in the order Coleoptera. Internal metamorphosis has as yet been studied only in such representatives of this order as, in the larval stages, have legs and antennae and eyes, and undergo a metamorphosis much less rapid and complete. Therefore, it should be important to learn whether this increasing periodicity in life history has produced the same changes here as in other orders, whether disappearance of larval appendages has resulted in the internal development of imaginal discs, whether rapid metamorphosis is accompanied by phagocytosis, etc.

The external signs of internal metamorphic processes begin to

[1] Dr. C. V. Riley found four larval stages in the clover leaf weevil. *Vide*, "The Clover Leaf Beetle Phytonomus punctatus Fabr.," *Rept. U. S. Dept. of Agric.* for 1881, pp. 171–179, Pl. X. The Phytonomus larva is less degenerate.

appear almost as soon as the larva is done feeding. There is a slight loosening of the cuticle, and contraction of the body away from it, especially on the dorsal side of the thoracic segments and of the head. The budding legs and wings, already visible through the transparent skin (Fig. 1), begin to grow and extend downward. The fat at the interior end of the body begins to lose its mottled, slightly grayish appearance, and becomes homogeneous, translucent, slightly yellowish-white.[1]

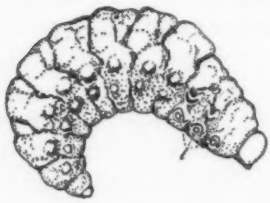

FIG. 1. — Full-grown larva of the flag weevil (*Mononychus vulpeculus* Fabr.). *w*, wing buds, and *l*, leg buds, as seen through the skin.

Then the larval skin is cast, and the pupa appears with all the adult appendages clearly recognizable. After this the progress of internal changes may best be gauged by pigmentation; first, in the eyes, then in the tips of the hind wings, and lastly in the general integument. Some of the corresponding internal phenomena will be discussed under the following headings.

II. *The Hypodermis during Metamorphosis.*

The hypodermis of this weevil is not, so far as observed, destroyed during metamorphosis to be again rebuilt in any part. The cells, however, while maintaining fairly constant relations at their ends, externally with the covering cuticle and internally with the tenuous basement membrane, take on remarkable variety of form and show a fine capacity for shifting, massing, or scattering themselves, previous to the definitive formation of the adult chitin. This might have been anticipated, in view of the exquisite sculpture and ornamentation of the adult beetle. It will be of interest to consider first briefly the origin of the appendage buds ("imaginal discs").

Wings and legs appear at the beginning of the third larval stage, each as a slight thickening of the hypodermis, showing almost from the beginning a slightly concentric arrangement of the elongating cells. Fig. 2, *B*, shows the beginning of a middle

[1] Correspondingly it ceases to be stained black with osmic acid in fixation.

leg. A wing bud would differ only in having the inner surface of the hypodermis free from tracheae, etc.

The striking difference between the behavior of the cells in these buds, and the behavior of hypodermis cells elsewhere (observed, doubtless, by every one who studies sections of insect larvae), I have thought it worth while to emphasize in this figure. Fig. 2, *A*, shows the crumpling which precedes molting everywhere except in these buds. Fig. 2, *B*, is a bud, and shows instead the thickening of the hypodermis and the compression of its cells. Elsewhere the hypodermis stretches as it grows;

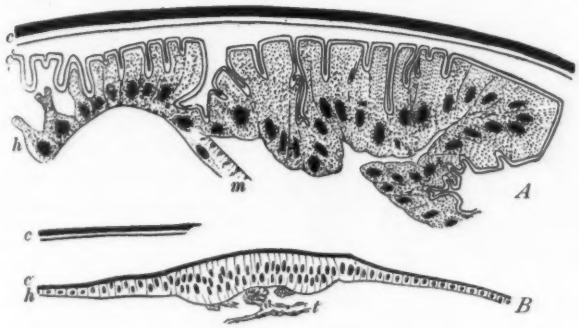

FIG. 2. — Two dispositions of hypodermis. *A*, vertical section of the frons at the end of the second larval stage, showing the crumpling of the hypodermis. *B*, vertical section of the bud of the middle leg at the time of molting at the end of the second larval stage, showing the thickening of the hypodermis, without crumpling. *c*, old chitine; *c'*, new chitine; *m*, developing muscle fiber; *t*, trachea.

the cells separate as they multiply; and that is true also of the hypodermis of the appendages, later, when the time has come for their extension. This we call retarded development, but the physiological explanation of it is still lacking.

There is no invagination of wing and leg buds in this beetle. Even the shallow hypodermal pockets formed about them in the more generalized Coleoptera are absent. The buds do not retreat from the surface. Fig. 1 shows their appearance as seen through the thin integument of the full-grown larva. Fig. 3 is a section of the wing at this time. The inner wall of the projecting shelf of hypodermis below the wing tip is all there is to represent the so-called "peripodal membrane." With

metamorphosis the wing begins to elongate from its apex and soon crowds downward past the shelf; and even before the casting of the last larval skin the general form of the adult elytron with the principal furrows upon its surface will have appeared.[1]

The scales of this weevil are wholly developed during the pupal period. They vary in form from simple sensory hairs as in the antennal club, and slender, lanceolate, sensory scales in the tarsal brushes, to flat, longitudinally fluted, Lepidopter-like scales of yellow and black colors on the dorsal and more exposed surfaces, and delicate, short-plumose, white, or pale yellow scales on the less exposed surfaces. These, one and all, arise from ordinary, single hypodermis cells, after the manner of the development of the scales in the lepidopterous wings, as described by Mayer[2] *et al.*

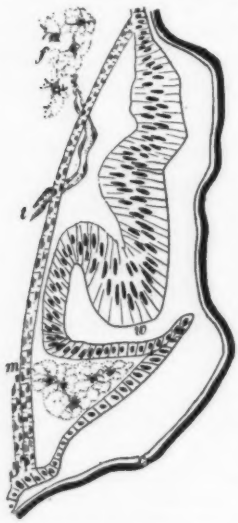

FIG. 3. — Vertical section of the fore wing in a grown larva. *w*, the wing apex; *c*, the loose chitine; *m*, muscle; *t*, trachea; *f*, fat.

First, in early pupal life the cells destined to produce the scales become much larger than their fellows and retreat a little from the surface, so that their nuclei appear at a lower level than the level of the other nuclei. Then each scale mother-cell loses its attachment to the basement membrane, becoming rounded off internally and sometimes acquiring a vacuole, and puts forth a process (the scale that is to be) between the adjacent surface cells (*cf.* Fig. 9). From this process the scale develops, the peculiarities of its own scale kind differentiating rather tardily.[3]

[1] There is no need to recount the wing development, since in all important features it is the same in this beetle as in a Coccinellid of which Professor Comstock and I have hitherto published an account (*Amer. Nat.*, vol. xxxiii, pp. 845–858, 1899).

[2] Mayer, A. G., "The Development of the Wing Scales and their Pigment in Butterflies and Moths," *Bull. Mus. Comp. Zoöl.* Vol. xxix, pp. 209–236, 7 plates, 1896. (Gives bibliography of earlier studies.)

[3] By far the most interesting features of the hypodermis are found in the metamorphosis of the head and the development of the rostrum. These will

III. *The Development of the Legs.*

Aside from a few not very recent accounts of the development of the legs in Diptera, in which the leg buds are deeply invaginated in the larva, Gonin's account of them in the butterfly Pieris remains the only considerable one. And in Pieris there are larval legs, well developed and functional from the first. It

FIG. 4. — Longitudinal section of the middle leg in a grown larva. *f*, fat; *l*, leucocytes; *e*, embryonic cells. (Drawn from a preparation made in my laboratory by Mr. C. Betten.)

will be well, therefore, to notice here some points in the development of the legs of this weevil.

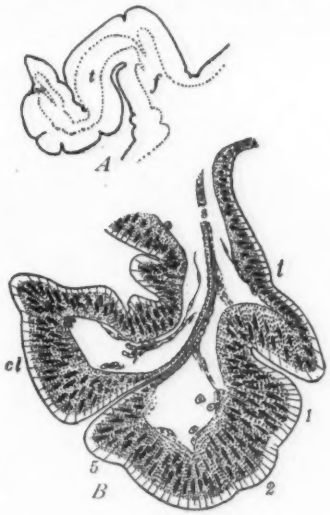

FIG. 5. — The leg of a larva, just before pupation. *A*, the entire leg in outline, and in part in optic section. *B*, a longitudinal section of the tarsus. *f*, femur; *t*, tibia; *1*, *2*, *3*, *5*, tarsal segments; *cl*, claw; *s*, developing tendon.

We have already called attention to Fig. 2, illustrating their origin. Fig. 4 is a longitudinal section of the leg of a grown larva, such as is shown in Fig. 1. Three principal divisions of the leg are already marked out by two deep constrictions. From the time of the beginning of the metamorphosis the growth of the legs is extremely rapid. Fig. 5, *A*, represents one of them as it appears after stripping off the larval skin just before pupation. (Fig. 8 shows wing and leg together, and in their relations to other parts.) The nine segments of the leg are

constitute the subject of another paper, which is now being prepared by a student in my laboratory.

now clearly recognizable, all save one — the fourth segment of the tarsus, whose size is small in the adult, and whose suppression thus seems to extend back into the ontogeny of the species. Fig. 5, *B*, represents a longitudinal section through the tarsus at the same stage. This shows well the condition of the hypodermis at the time when all is ready for that great extension which accompanies pupation. Here is shown also the development of the strong tendon which protracts the claw, as a hypodermal invagination between segment five of the tarsus and the base of

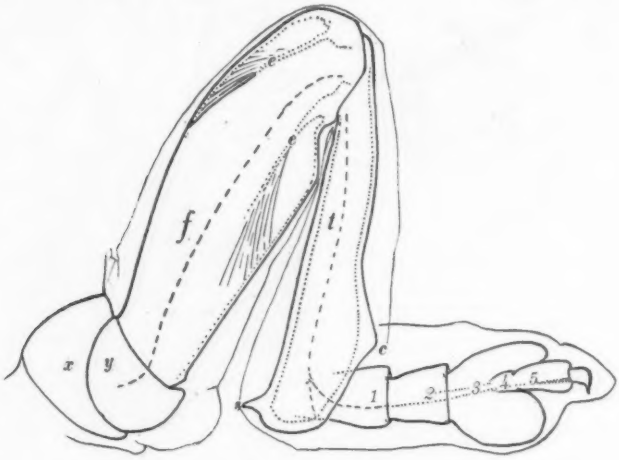

FIG. 6. — Leg of young pupa, within the pupal skin, in part in optic section. *x*, coxa; *y*, trochanter; *f*, femur; *t*, tibia; *c*, corbel; *s*, scrobe; *e*, *e*, developing tendons (flexor and extensor tibiae) and muscles; *1*, *2*, *3*, *4*, *5*, segments of the tarsus.

the claw. At pupation this tendon is drawn out to great length, the hypodermis nuclei move apart, and spend themselves completely in chitine formation. Thus is the tubular ingrowth of soft hypoderm cells transformed into a solid cord of chitine. Muscle cells developing internally at the expense of the fat are from the first intimately associated with these hypoderm cells (*cf.* Fig. 9), and through them become attached later to the tendon. Just after pupation there is a striking similarity in appearance between these tendons growing from the surface into the leg cavity and the tracheae growing from the body cavity into it.

Fig. 6 shows the leg of a young pupa within its sheath. All the leg segments are rapidly assuming their definitive form. The fourth tarsal segment has reached its maximum development; it will be relatively smaller in the adult. The broad, flat, brush-bearing pads of the third tarsal segment are here big bag-like dilatations. Corbel and scrobe are very evident upon the tibia, and the femur and other segments are full of fat, rapidly being metamorphosed into muscle.

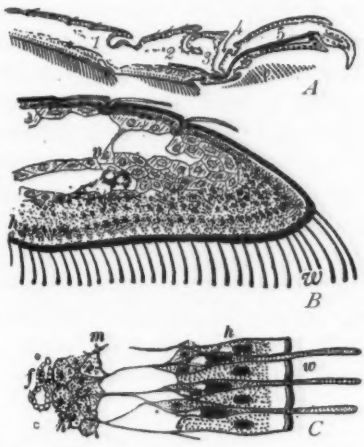

FIG. 7. — The tarsus in the pupal stage. *A*, longitudinal section of the tarsus in an old pupa. *B*, part of another section from the same series passing through one of the brushes of the 3d segment; *w*, the scales constituting the brush; *v*, the edge of one of the brushes belonging to the third segment; the tendon which retracts the claw is drawn in solid black; *n*, neuroblasts. *C*, a bit of a section through the tarsal brush in a young pupa, to show the origin of the scales; *w*, the scales; *h*, hypodermis; *m*, basement membrane; *n*, neuroblasts (undifferentiated); *f*, fat.

Fig. 7, *A*, represents the structure of the tarsus in an old pupa; externally it is practically that of the adult beetle. Fig. 7, *B*, is another section in the same series, passing through one of the lateral pads of the third tarsal segment. It shows a thinner hypodermis above, bearing scattered scales, and a thicker hypodermis below, bearing the dense tarsal brushes. Within are seen disintegrating fat cells, and other growing cells, angular and with large nuclei, which I take to be neuroblasts. Fig. 7, *C*, is from a younger pupa. It shows well the manner of development of the tarsal brush. The mother-cells of its constituent scales settle below the general level of the hypodermis; owing to close crowding, their nuclei take on a cuneate form, and on the inner side of each a minute but distinct vacuole appears. At this age the hypoderm cells generally, as here, reach their basement membrane by long, peaked internal processes. Against this basement membrane here lie heaped embryonic cells, which later differentiate as the above-mentioned neuroblasts. Subse-

quent approximation of hypoderm cells and basement membrane (due, shall we say, to the drawing in of the peaked processes?), together with the loss of distinct cell boundaries in the hypodermis, renders the relation of parts much less clear in the later stages.

The tarsal claw and the tibial scrobe are developed alike from thick projections of hypodermis cells, forming at first a blunt point, which becomes sharp and takes on its characteristic tenacular curvature only when the chitine begins to harden. The corbel, however, being formed not at an angle of the leg, but upon an originally smooth surface, develops differently. There is a dense heaping of the hypoderm cells along what is to be the rim of the *U*-shaped corbel, among which the very large mother-cells of the fringing spines are early differentiated. Within the rim the cells are few, slender, and scattered. Outer (cuticle) and inner (basement membrane) surfaces are at first parallel; but the subsequent settling down of all the hypoderm cells upon their basement membrane leaves, where the few slender cells were within the rim, the proper concavity of the corbel.

IV. *Fat.*

The extraordinary growth taking place during the last larval stage is due almost wholly to the accumulation of fat. This occurring chiefly upon the dorsal side brings about the characteristic curvature of the larva. Hardly has growth been completed, however, before the reverse process sets in; the fat begins to be demolished and used in the construction of new parts. The external appearances accompanying the reduction of the fat have already been described. In sections the appearance is that of local disintegrations of the periphery of certain of the fat masses. Fig. 8 is a section through the middle of the thorax very near the beginning of metamorphosis. At the bases of the budding appendages and immediately above and below the alimentary canal, the fat is disintegrating. The appearance is that of the melting of frost. The fluid *residuum* flows forward into the head and laterally out into wings and legs, bearing along floating islands broken away from the fat masses.

During growth the fat is being stored in undifferentiated mesodermal cells which are free within the body cavity. These cells become greatly distended with the fat globules, which come to fill great interstices in the protoplasm toward the cell periphery. That each nucleus retains its vitality notwithstanding, is shown by its staining reactions, and by its retention of a central mass of protoplasm about itself, from which the peripheral strands that encircle the fat globules proceed. This is certainly not typical fatty degeneration; it seems to me much more properly considered to be partial anabolism, affected by these cells in their rapid elaboration of hydrocarbons during the transient period of abundant food supply. This view is corroborated by their later history. They do not (at least a majority of them do not) die with the dissolution of the fat. Nothing is plainer while one is watching the disintegration of the fat masses than that the nuclei contained therein show none of the usual signs of necrobiosis. Here and there will be seen a nucleus which, together with its enveloping coat of protoplasm, seems to be slipping itself free from its aforetime accumulation of fat. Furthermore, these nuclei thus isolated can be seen associating themselves with the developing muscle rudiments, and, apparently,

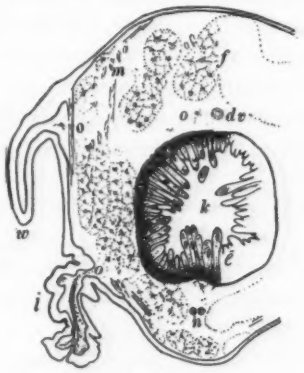

FIG. 8. — Partial cross-section of a larva, nearing pupation. *w*, fore wing; *l*, middle leg; *m*, muscles; *f*, fat; *dv*, dorsal vessel; *k*, alimentary canal; *e*, digestive epithelium, ready for dissolution; *n*, nerve cord; *o*, *o*, *o*, areas of first disintegration of the fat masses.

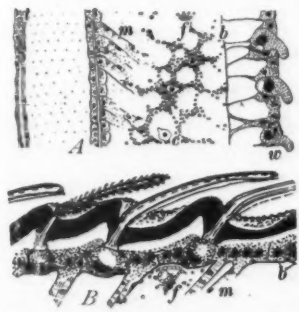

FIG. 9. — The development of scales and of muscle fibers. *A*, a bit of a longitudinal section of the femur of a young pupa; *t*, developing trachea; *s*, developing tendon (flexor tibiae); *m*, developing muscle fibers; *f*, disintegrating fat; *c*, a nucleus belonging to the fat mass isolating itself from the same; *b*, basement membrane; *w*, developing scales, in the midst of ordinary hypodermis. *B*, a bit of the body wall from a newly transformed imago, lettered as in *A*.

themselves becoming the nuclei of new muscle fibers. The single fat globules which they often carry with them and sometimes retain, even after they have become associated with the muscle rudiments, enable one to follow them easily from their former situation into this new one.

There is no destruction of any larval tissue by phagocytes during metamorphosis, but *after the imago stage has been entered upon*, large numbers of phagocytes appear in the midst of the fat along the sides of the abdomen. There are numerous embryonic or undifferentiated cells lying along the sides of the body in the larvae; and these, I believe, begin to penetrate the fat masses toward the end of the pupal stage. Fig. 10 shows the appearance they present in a recently transformed weevil. Up to this time the fat filling the abdomen has not been greatly reduced, except in the anterior end; the change of form in the abdomen in passing from larva to imago is slight as compared with that of other parts. But it is clear that the internal metamorphosis is only well under way when the external is completed. This reserve store of fat is for the completion of the still weak organs of the imago, and for nutrition during the ten long months of inactivity remaining before the flags bloom and feeding begins again.

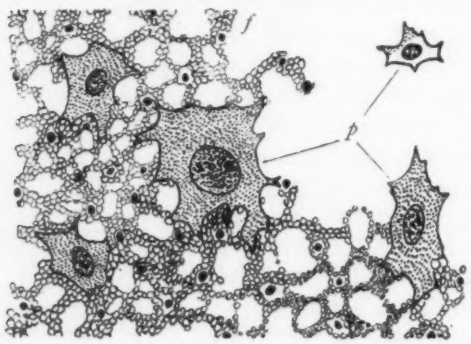

FIG. 10. — Phagocytes attacking the fat; the section is through the abdomen of a recently transformed imago. *p*, phagocytes; *f*, fat. (From a preparation made in my laboratory by Miss Elizabeth Andrews.)

After calling attention to some of the interesting features of post-embryonic development, I would not close this little paper without mentioning the exceptional availability of this species for laboratory study. On a single trip to a favorable flag clump during the latter part of July in this latitude, one may gather in

a little while enough material for studying its entire metamorphosis. This material may be excellently fixed in boiling 70 per cent alcohol, and in all stages preceding the imago the chitine is so thin as to interfere but little with section cutting.

The following conclusions from the foregoing study are believed to be new:

1. In *Mononychus vulpeculus* Fabr. there are three larval stages.

2. The full-grown larva is very degenerate, having only the merest rudiments of antennae, eyes, optic lobes, and salivary glands.

3. The greater part of the increase in size takes place in about a week after entering the third larval stage; it is due mainly to fat accumulation.

4. This brief period of feeding and rapid accumulation of half-assimilated food material is correlated with an extremely long final assimilation period, lasting through months of imaginal life.

5. There is no real invagination of the buds of wings or legs.

6. Many nuclei of fat cells persist after the dissolution of the fat masses, free themselves from these masses, retaining about themselves an investment of protoplasm, associate themselves with developing muscle fibers, and, probably, themselves become the nuclei of new muscle fibers.

7. Phagocytosis, which was observed only in the fat masses along the sides of the abdomen, occurs only after external metamorphosis is complete.

NOTES ON THE PHYSIOLOGY OF REGENERATION OF PARTS IN PLANARIA MACULATA.[1]

C. C. LEMON.

I. *Modes of Regeneration.*

In Planaria maculata there are two methods of inducing regeneration. First, isolated parts of sufficient size taken from any part of the body except the region in front of the eyes will regenerate; and second, partly isolated areas may regenerate, producing compound planarians.

1. *Isolated Parts.* — Randolph,[2] 1897, states that when a worm was cut into eight pieces by cross cuts, seven of them lived, and six of them regenerated all lost parts. The seventh failed to regenerate eyes.

Morgan[3] has shown that there is a limit of size below which regeneration of lost parts will not take place. He also thinks that while the area in front of the eyes, which does not regenerate, is near this lower limit of size, there is another cause, probably that of greater specialization, why it will not regenerate lost organs.

My own observations on regeneration of isolated parts, though limited, for the most part support those of Morgan, as will be seen from the following record of experiments. A worm 10 mm. long and 2 mm. to 3 mm. in width was cut into

[1] The work herein recorded was done in the Laboratory of Experimental Morphology of Michigan University, under the direction of Dr. F. R. Lillie, to whom the writer wishes to express his sincere thanks for assistance and encouragement.

[2] "Observations and Experiments on Regeneration in Planarians," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. v, p. 355. 1897.

[3] "Experimental Studies of the Regeneration of Planaria maculata," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. vii, pp. 365-372. 1898.

eight pieces as nearly equal in size as possible. All pieces regenerated lost parts and became fully developed worms in about ten days at ordinary room temperature. Another worm 5 mm. long and 1 mm. wide was cut into eight pieces. The operation was, however, so delicate that there was not much certainty in obtaining uniform size of the pieces. The larger pieces regenerated the lost organs, while the smaller ones did not. Just what the limit is, was hard to ascertain, as the relation of the piece to the whole could not be accurately determined, on account of its constantly varying shape. Parts which, by the most careful measurements, were shown to be about one-twelfth of the size of the original animal, regenerated and became fully formed planarians, while those of smaller size did not. Experiments on sixteen worms resulted in the same way. The area in front of the eyes did not regenerate in a single case.

2. *Production of Compound Planarians.* — This may be brought about in two ways: (1) Parts separated by cuts made along or near the middle line will generally complete themselves by regeneration without much growth. (2) Even extremely minute strips partly isolated may grow out like buds, and when of sufficient size, develop the characteristic organs of the species.

There is, of course, no line of demarcation between these two ways, which are united by a series of intermediates.

a. *By Regeneration.* — When a worm was split through the middle line of the anterior part of the body, sometimes the partly isolated left half regenerated a new right half and the partly isolated right half a new left half, thus producing a worm with two complete heads (Fig. 1). A similar operation may be performed on the posterior part of the body, resulting in two tails (Fig. 2). The time required for the regeneration of two heads is fifteen to twenty days, varying somewhat according to temperature. The regeneration of double tails occurred in five to ten days.

On Dec. 24, 1898, a large planarian was operated on by splitting the tail, as indicated in Fig. 13, except that the cut did not extend through the pharynx but only to the region

just posterior to it. On Jan. 3, 1899, two fully formed tails had developed. On January 5, the animal divided by fission about 3 mm. in front of the point of union of the two tails. The part possessing the two tails regenerated a new head, producing the animal seen in Fig. 3.

On January 11, the anterior part of the worm was again split posteriorly, this time dividing the pharynx. Five days later, on January 16, the posterior end of the worm again divided off, and subsequently regenerated a new head, as seen in Fig. 4. The third and most anterior part of the original worm was split posteriorly, but the double tails

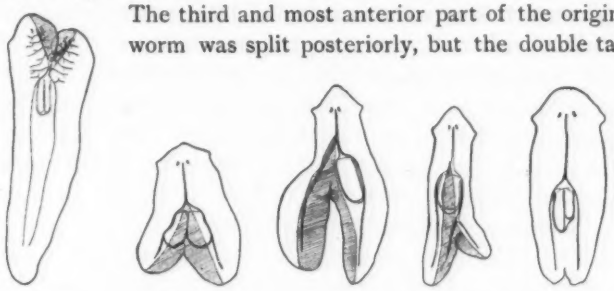

FIG. 1. FIG. 2. FIG. 3. FIG. 4. FIG. 5.

FIG. 1. — A double-headed planarian caused by regeneration after the original head had been split.
FIG. 2. — A planarian with two tails resulting from splitting and regeneration.
FIG. 3. — A planarian which separated from that of Fig. 5 by fission after its tail had been split.
FIG. 4. — This worm also separated from that of Fig. 5 by fission eleven days after Fig. 3.
FIG. 5. — The head end of the worm from which those in Figs. 3 and 4 separated.

could not be produced again, although the operation was performed three times. The only result that could be obtained was a worm with a slightly bifid tail and double pharynx (Fig. 5).

An interesting feature of the experiment with this worm is the way in which the alimentary canal developed in the regenerated parts. The left tail of Fig. 3 is supplied with nutriment by means of a sub-branch which comes off from the anterior branch of the canal, while the original left branch of the canal, which was severed in the operation, has disappeared. On the other hand, the right tail of Fig. 4 receives its nutriment by a sub-branch from the right posterior branch of the canal, which still persists, or is possibly a new formation. This and other problems concerning the anatomy of compound planarians are of interest and should be worked out.

b. *Budding.* — Small strips of tissue from the margin of the body or edge of a cut resemble buds in their capacity for growth and differentiation. These false buds regenerate more rapidly than larger portions of the body. To induce the growth of buds an incision is made, partly severing a very narrow strip (.5 mm.) of tissue, as shown by the lines in Figs. 6 and 10; Fig. 6 *a* indicates the method by which the worms in Figs. 8 and 9 were produced, and Fig. 10 *a* indicates how Figs. 11 and 12 originated.

In Fig. 7 the cut was made as indicated by the dotted line *a*. The bud, which was 4 mm. long, regenerated a new head, with brain, eyes, and cephalic lobes, in fourteen days. This head was developed from tissue in the posterior third of the body. Dalyell,[1] referred to by Randolph, thought that heads could be developed from tissue of the anterior part of the worm only. This idea is wholly disproved by Figs. 7, 11, and 12. At *b*, Fig. 7, is seen a bud one day after being cut.

i. *Growth.* — The bud, not having sufficient muscular strength to right itself against the larger part of the worm, heals without uniting with it, as is the case so often with animals split in the middle line. Growth begins very soon after the operation, being quite perceptible at the end of two days. It occurs in two ways: first, by regenerating new tissue on the cut edge of the bud; and second, by the increase of length, breadth, and thickness of the old tissue.

ii. *Differentiation of New Organs.* — Along with the increase in size the body becomes rounded off on the dorsal surface, and the head becomes broader and thicker in the region of the brain area when the cephalic lobes appear. Finally the eyes and pharynx, where a pharynx is developed, appear almost simultaneously.

In Fig. 8 the bud was formed by partly isolating a narrow strip of tissue from the side of the anterior part of the animal, as indicated by the shaded part *a*. About the time the cephalic lobes appeared, which was twelve days after the operation, the bud began to assert its independence, and was dragged about by the stronger worm with its head extending in a pos-

[1] "Observations and Experiments on Regeneration in Planarians," p. 370.

terior direction. As a result of the tension caused by the pulling, growth took place in the region *a* (Fig. 8), making the position of the posteriorly directed head a permanent and natural one.

In the case of Fig. 9 the bud was produced in the same way, but from day to day as the tension increased a slight cut was made at *a*, and as a result we do not have the head end of the bud directed posteriorly to the main axis of the worm, but nearly at right angles to it. The cutting prevented growth, and hence, when the animal comes to rest, or when relaxed in

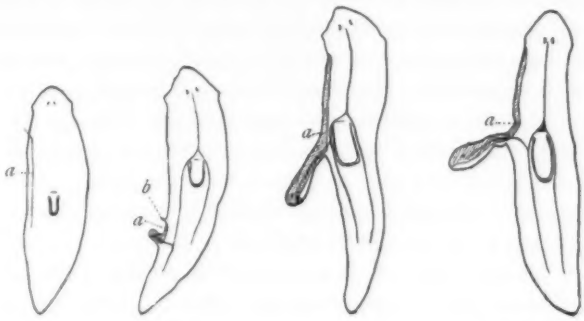

FIG. 6. FIG. 7. FIG. 8. FIG. 9.

FIG. 6. — At *a* is seen the kind of cut which was made to produce buds.
FIG. 7. — A head regenerated from a bud, and a bud, *b*.
FIG. 8. — Pseudoheteromorphosis.
FIG. 9. — Frequent cutting at *a* prevented pseudoheteromorphosis in the worm of this figure.

killing, the bud, instead of remaining in a posteriorly directed position as when in motion, takes a position more nearly the same as that which it originally occupied.

While the bud was developing, the cut edge of the larger part regenerated enough new tissue to replace that which went to produce the bud. Thus we have a well-formed double-headed planarian in the case of Fig. 8. In Fig. 9 the bud failed to develop a left eye. This may be due to the frequently cutting at *a*; otherwise our present knowledge of the case makes it impossible to decide what the cause may be.

iii. *Final Fate of Parts.* — One point was quite noticeable in all the experiments with buds. When the animal had be-

come well formed there was a strong tendency to divide and in this way get rid of the abnormal condition. Ignorance of this fact cost the writer two of his best examples of regeneration; and it was only by diligently watching their development and killing the material at the proper time that the examples for this part of the paper could be obtained.

II. *Heteromorphosis.*

1. *Historical.* — Randolph[1] mentions four cases found by Dalyell in 1811 which are worthy of mention here. The first was a planarian with a bifid tail, between the two branches of which was an erect structure supporting a head. Second, a planarian, upon the side of which incisions had been made, developed a head pointing downward in the direction of the tail. The third and fourth cases consist of two monstrosities, the description of which is quite similar to that of Fig. 11. These were two worms, each of which had another attached to it and lying at right angles to its tail.

Van Duyne[2] gives three figures which he claims prove the possibility of heteromorphosis in the planarian. One, his Fig. 3, represents a worm with two heads on the anterior part of the body, one of which points posteriorly. The second one, his Fig. 4, shows a worm whose body has been split through the tail almost to the head. Between the two tails thus produced two heads have appeared, which, when the tails are widely separated as represented in the figure, point in a posterior direction. And lastly, his Fig. 5 represents a tail pointing in an anterior direction.

Morgan[3] gives one example of apparent heteromorphosis, his Fig. 36. It shows a worm with two heads, which point

[1] "Observations and Experiments on Regeneration in Planarians," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. v, p. 367.

[2] "Ueber Heteromorphosis bei Planarien," Separat-Abdruck aus dem *Archiv für die ges. Physiologie.* Bd. lxiv, Taf. x.

[3] "Experimental Studies of the Regeneration of Planaria maculata," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. vii, p. 381.

in opposite directions when in a relaxed condition, but when expanded form an angle of about 100°.

Morgan[1] has confirmed Spallanzani's discovery of earthworms regenerating a tail in place of a head. Sections of these worms show a ventral cord extending to the new part, that no brain is present, and that the nephrostomes in the new part are turned backward towards the old part.

Loeb,[2] in his investigations to determine the cause of animal forms, produced monstrosities with hydroids in which the oral end was regenerated on the aboral end. Loeb proposed the term "heteromorphosis" for such monstrosities. Heteromorphosis not only includes the regeneration of a head in the place of a tail, but of any organ in any place where in nature one of unequal value would occur, as arms from the hips and legs from the shoulders, etc. Loeb defines heteromorphosis as "the replacement of one organ by another physiologically and morphologically different."

2. *Analysis.* — The term "heteromorphosis" thus includes the entire reversal of axial relations as well as the development of any single organ in place of another. It will be useful to distinguish these as polar heteromorphosis and heteromorphosis of single organs. Examples of the latter are found in various forms, as the regeneration of a tentacle-like organ in place of an eye in crabs, etc. Examples of polar heteromorphosis, on the other hand, with few exceptions, occur only among the Coelenterates.

Cerfontaine,[3] in his "Observations physiologiques sur l'Astroides calycularis," records the regeneration of a crown of tentacles on the base of a severed part of a polyp.

Loeb has found axial heteromorphosis to be quite common among the coelenterates and has been able to produce it in

[1] "A Confirmation of Spallanzani's Discovery of an Earthworm Regenerating a Tail in place of a Head," Abdruck aus dem *Anatomischen Anzeiger*. Bd. xv, pp. 407–410. 1899.

[2] *Untersuchungen zur physiologischen Morphologie der Thiere*. Bd. i, ii. Wurzburg, 1891.

[3] "Notes préliminaires sur l'organisation et le développement de différentes formes d'Anthrozoaides (deuxième communication)," *Bull. de l'Acad. Roy. des Sci., des Lettres et des Beaux-arts de Belgique*. No. 8, Notes v–viii. 1891.

at least the following forms: Tubularia mesembryanthemum, Aglaophemia pluma, Plumularia pinnata, Eudendrium (rasimosum ?), Sertularia (polyzonias ?).

Bickford and Driesch,[1] cited by Morgan, have also shown that in the tubularian hydroids two heads may develop on opposite ends of a piece cut from a stem, especially if the piece be short.

3. *Pseudoheteromorphosis.* — By cutting a narrow strip from any part of the body so as partly to isolate it, a posteriorly directed head may be developed by the reversal of the piece.

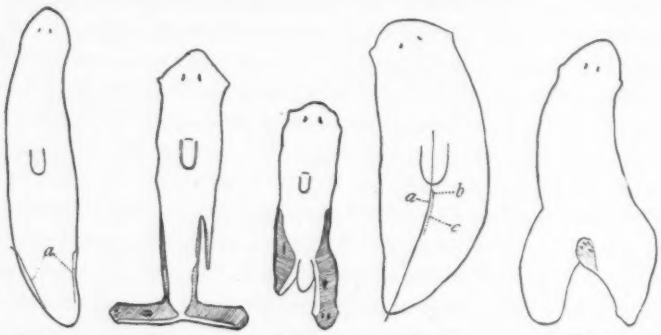

FIG. 10. FIG. 11. FIG. 12. FIG. 13. FIG. 14.

FIG. 10. — The lines *a* show the nature of the cuts which produced heads at right angles to the body.

FIG. 11. — A worm with heads lying at right angles to the main body.

FIG. 12. — Pseudoheteromorphosis.

FIG. 13. — The lines *a*, *b*, and *c* represent the cuts made to induce regeneration of heads in the tail region.

FIG. 14. — A head regenerated on one of the tails.

If by tension and growth this position becomes permanent, forms are produced which, to the casual observer, appear to be marked examples of heteromorphosis. Figs. 8, 12, 15, and 16 possess all the outward appearances of true heteromorphosis, but by the aid of Figs. 6, 10, and 13 one can readily show that there is neither the reversal of axial relations nor the development of one organ for another. Hence we do not have true heteromorphosis, but simply the swinging around of a portion

[1] "Experimental Studies of the Regeneration of Planaria maculata," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. vii, p. 382.

of tissue as a whole, so as to give the anterior end a posterior direction, or pseudoheteromorphosis.

Perhaps the best example of pseudoheteromorphosis is found in Fig. 15, which was produced in the following manner. On Dec. 22, 1898, the worm was operated on by splitting its tail, as indicated by the line *a* in Fig. 13. Then a small anteriorly directed piece of tissue was partly isolated on the inner margin of the right tail *b*, which developed a head, as seen in Fig. 14, by Jan. 9, 1899.

Fig. 15. — The worm of Fig. 14 in an expanded condition.

Fig. 15 represents the same worm in an expanded condition during locomotion.

Fig. 16 was produced in the same way as Fig. 15, except that the strip, which was isolated from the inner edge of the right tail, was cut longer, as indicated by the dotted line *c* in Fig. 13.

Neither Van Duyne nor Morgan gives evidence of having produced anything other than pseudoheteromorphosis.

4. *Critique of Evidence.* — In Van Duyne's first example of heteromorphosis (Fig. 3 of the plate) he figures a worm with two heads, one of which arose from the wound caused by taking a piece from its side by two cuts, a transverse one back of the right half of the head, and a longitudinal one from the inner end of the first cut to the tip of the tail.

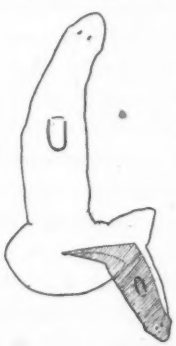

Fig. 16. — Pseudoheteromorphosis.

In order that this be an example of axial heteromorphosis it must have been regenerated from tissue which originally bore the same relation to the main axis of the worm as does the tail, *i.e.*, it must have been regenerated from tissue, the free end of which was originally posteriorly directed. The drawing does not clearly show this, but rather indicates that this head may have been regenerated on the anterior end of the newly formed tissue on the side of the worm and was forced to turn backward by the shoulder-like projection of old tissue.

Likewise in Fig. 4 of Van Duyne's plate there is no evidence that the heads may not have arisen from anteriorly directed tissue, as did the head in my Fig. 15. Fig. 5 of Van Duyne's plate gives no more evidence of being a tail than of being a partially developed head.

Morgan, in Fig. 36 of his paper, gives an example of what he considers to be axial heteromorphosis. He says: "The entire history of this piece is known, and there can be no doubt that two heads developed on opposite ends of the same cross-piece." Further he adds: "The bending of the heads to one side is due, in all probability, to the knife cutting somewhat obliquely to the long axis at the time that the piece was removed." May it not be more probable that we have here a case of the development of a head from each of the anterior corners of the piece? It is certainly reasonable to suppose this in the light of the evidence given. To determine whether this be an example of axial heteromorphosis or not, two things are necessary, *viz.*: (1) That we know the end of the piece which was originally directed anteriorly by some means other than the direction of its motion; and (2) that we know that the same end, which was the anterior end when the piece was first cut, continues to be the anterior end of the newly developed worm. Several cases were noticed where the piece, either from not having been cut squarely across or from some other cause, at first moved in a direction diagonal to its anterio-posterior axis, but afterwards, when the regenerated part developed normally, *i.e.*, in the line of the anterio-posterior axis, it again moved in a straight line. If the new tissue developed a little to one side of the anterio-posterior axis, as was sometimes the case, the piece continued to move in a diagonal direction, following the newly formed head. May not Morgan's Fig. 36 be an example involving conditions similar to these without involving axial heteromorphosis?

5. *Effect of Injury to One Part on a More or Less Different Part.* — In addition to the tendency to divide after the regeneration of new organs, referred to elsewhere, it sometimes happens that an operation on one part of the body produces an abnormality in some other part. Three interesting cases were

found where the eyes either divided, or became abnormally large and irregular in shape, and two where the pharynges developed abnormal proportions.

The first case was caused by an operation upon a planarian to produce a bud, as indicated in Fig. 6. Three times the bud divided off by fission, leaving the worm almost normal in appearance. After the third operation the eyes, which were crescentric in outline, began to deposit pigment in the concavity in irregular masses until the condition represented in Fig. 17 was produced, when the head separated from the body by fission.

The second case (Fig. 18) is that of a worm which had been operated on in a similar manner. The bud divided off and

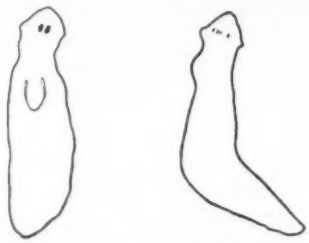

FIG. 17. FIG. 18. FIG. 19.

FIG. 17. — A worm in which the eyes have become abnormally large after being operated on.
FIG. 18. — A worm in which two new eyes developed after an operation upon its sides.
FIG. 19. — The dark part of the right eye divided after operation on the side of the worm.

almost immediately the eyes divided, giving four eyes. The one on the extreme left side of the head has the concavity on the right side, suggesting the possibility of its functioning as a right eye. Two others are in almost the normal position, while the fourth lies between them and a little to the left of the middle line of the head.

The third case (Fig. 19) is that of a worm which had been operated on in the posterior part of the body on the left side, producing a bud. When the bud had become half grown it divided near its anterior end. The right eye of the worm then divided in such a way as to produce two, one lying just anterior to the other. The head of this animal also separated from its body by fission soon after the division of the eye.

The two cases of abnormally developed pharynges were

found in two worms which had been split near the middle line of the body. One was split through the head back to the pharynx but not including it. After several operations two heads developed, and it was noticed that the pharynx was gradually increasing in width. This continued until the two heads were fully formed, when it had reached a size nearly twice that of the normal.

The other case was a worm whose tail had been split to the base of the pharynx. After the operation the pharynx increased continually in width until two tails were fully formed.

LABORATORY OF EXPERIMENTAL MORPHOLOGY,
MICHIGAN UNIVERSITY,
ANN ARBOR, MICH., July 28, 1899.

THE STRUCTURE OF THE EYE OF SCUTIGERA (CERMATIA) FORCEPS.

JOSEPHINE HEMENWAY.

GRENACHER ('80), in his article entitled "Ueber die Augen einiger Myriapoden," described the structure of the eye of Scutigera (Cermatia araneoidea). Briefly reviewed, his account is as follows:

Externally the eye of Scutigera has the appearance of a true facet eye, consisting of one hundred of these "facets." To each facet there corresponds an ommatidium. Each ommatidium consists of a central crystalline body, surrounded by three tiers of cells; the distal tier of pigment cells, the middle and proximal tiers of retinular cells secreting on their inner edges a narrow band, the rhabdom. The crystalline body is composed of very irregular segments. These segments may be either cells or cuticular structures. In the adult eye they cannot be regarded as cells, as nuclei are not found in them, although Grenacher admits that at some time in their existence they may have been cells, later becoming modified and losing their nuclei. The possibility of their being secretion products he does not admit, as he finds no cells to which their origin could be traced. There are six to eight or nine of these segments.

The retinular cells with their rhabdoms embrace the proximal two-thirds or three-fourths of the crystalline body, the posterior portion of the retinular cells reaching to the basal membrane. Of the three tiers of cells surrounding the crystalline body, the middle tier, or outer retinula, is made up of from nine to twelve cells; the proximal tier, or inner retinula, of three to four cells. Sections through the proximal layer show that at this level the rhabdom is made up of four parts. Toward the extreme proximal end of these proximal retinular cells only three with their rhabdoms are visible in cross-

sections, the fourth having been pushed out. The nuclei of the retinular cells lie in the distal portion. The pigmentation of the eye consists partly of the pigment granules in the retinular cells and partly in the separate pigment cells. Of the latter there are three distinct groups: (1) a circle of from eight to ten large flattened cells, the outer tier of my description around the outer part of the crystalline body; (2) long, spindle-shaped pigment cells situated between the ommatidia, extending to the inner cuticula; (3) a third group, the supplementary cells of my account, is found on the posterior part of the retinula, between the retinular cells.

Grenacher also mentions the pigmentation of the optic nerve and the "inner cuticula."

Adensamer ('93), in his studies on this eye (Scutigera coleoptrata), confirms and completes Grenacher's statements. He differs in certain points.

The cornea of each ommatidium Grenacher regarded as externally convex, although there were individual differences. These differences Adensamer regards as stages in the development of the cornea.

In the adult eye frequently there were found in the crystalline body large yellowish enclosures, which had the appearance of fat drops. These are not to be confused with the nuclei for which Grenacher looked. Of the segments he found from seven to nine.

But in an individual 5 cm. long Adensamer states that he found nuclei in the crystalline body; thus he feels justified in calling the segments "cells."

As to the nerve fibers he was more successful than Grenacher, in that he saw the connection of the fiber with the outer and inner row of retinular cells. This he proved by sections. Just under the basal membrane there is a nerve connected with a muscle, which is entirely distinct from the optic nerve. Adensamer believes that this was probably mistaken by Grenacher for the real optic nerve. The latter consists of a bundle formed of the separate nerve fibers meeting proximal to the basal membrane.

Speaking of the superficial resemblance of the eye of Scutigera to that of insects and crustaceans, and the actual differ-

ences between them, Adensamer suggests calling the eye of Scutigera a "pseudo-facet" eye. Rosenstadt ('96) discusses the question as to whether the eye of Scutigera can be regarded as a true facet eye, reviewing the arguments of Grenacher and Adensamer. He also suggests a way by which an eye, as that of Scutigera, could be developed from a true facet eye.

The following work was done in the Biological Laboratory of Bryn Mawr College, under the direction of Prof. T. H. Morgan, to whom I am greatly indebted for valuable suggestions and criticism.

The species studied was Scutigera (Cermatia) forceps.

For sectioning, the best results were obtained by hardening the fresh material in corrosive acetic for fifteen minutes, then running it up through the successive grades of alcohol.

The dense pigment obscured all details, therefore a depigmenting agent, as KOH, was used (*cf.* Parker, "The Eyes in Scorpions," '87). The preparations were stained with iron-haematoxylin.

As a maceration fluid, a modification[1] of Béla Haller's fluid was used. Material left in it for a year gave excellent results. The separate ommatidia fell apart, and by gently tapping the preparation the individual cells of each ommatidium could be isolated.

By this means I have been able to make out more definitely the structure of the different component cells than have the authors mentioned above, and in some respects have been able to add some points to their results.

The eye of Scutigera forceps is nearly triangular in shape. The corneal hypodermis is faceted, one ommatidium corresponding to each facet. Each eye is composed of about two hundred individual units or ommatidia.

Fig. 1 *A* shows[2] a single ommatidium, its proximal end bordering on the inner cuticula or basal membrane.

[1] Béla Haller's mixture modified: two parts glacial acetic acid; two parts water; one part glycerine.

[2] The figures are all camera drawings: Fig. 1 *A* and *B* were drawn with a No. 7 objective; Fig. 1 *C* and *D* were drawn with an oil immersion $\frac{1}{12}$; Fig. 2 *A*, *B*, *C*, *D*, *E*, *F* were drawn with an oil immersion $\frac{1}{12}$.

Surrounding each ommatidium are elongated pigment cells, extending the entire length of the ommatidium (Fig. 1 *B*). At both distal and proximal ends these pigment cells become expanded, the pigment granules collecting in the expanded portions. At the proximal end this gives the pigmented appearance of the basal membrane, spoken of by Grenacher.

There are sixteen to eighteen of these pigment cells belonging to an individual ommatidium. The nuclei are visible without reagents, but are more clearly shown by methyl green.

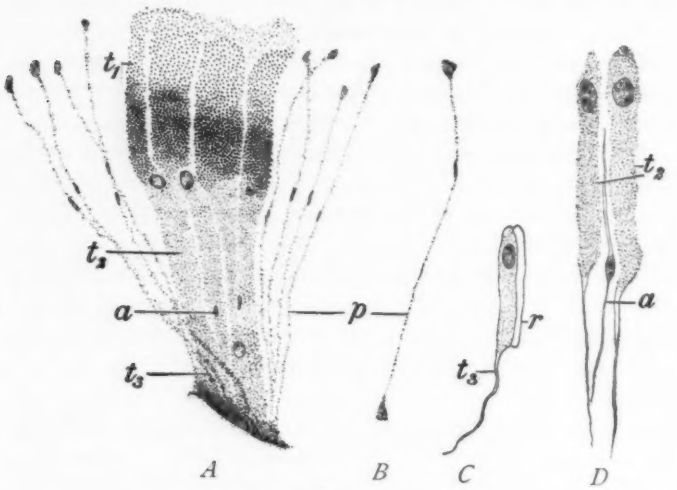

FIG. 1.

They are found at the same level as the nuclei of the middle tier of cells (Fig. 1 *A*). Each ommatidium consists of a clear, crystalline body, surrounded by three tiers of cells; the outer consisting of twelve (t_1), the middle of ten to twelve (t_2), and the inner tier of three to four cells, respectively (t_3).

The cells of the outer tier are large and flat and deeply pigmented at the proximal ends, the pigment granules being extremely large and round. The nuclei did not show in a macerated specimen, owing to the pigment.

The middle tier of cells are called by Grenacher the "outer retinular cells." They are longer and more narrow than the

cells of the outer tier, reddish in color, lacking the black pigment of the outer tier.

(Fig. 1) *D* t_2 shows two of these cells with the nuclei at the extreme distal portion. At the proximal end each cell is prolonged into an extremely fine "tail," which runs down between the cells of the inner tier and is continued through the basal membrane as a nerve fiber.

The cells of the inner tier have their proximal ends bordering upon the basal membrane. From the proximal ends fine processes continue through the basal membrane to form the nerve fibers. The cells are much broader than those of the middle tier.

Cross-sections through the different levels show the crystalline body occupying the central axis of the ommatidium, surrounded by a clear zone or rhabdom forming the inner parts of the cells of the ommatidium (Fig. 2 *B*, *r*). The clear zone is formed of the structures called by Grenacher the rhabdoms — a secretion product of the retinular cells. In macerated specimens these rhabdoms were visible upon the inner surface of each cell of the two proximal tiers (Fig. 1 *C*) and could be made to separate from the cell by tapping. The "tail," or nerve, is on the opposite side of the cell from the secreted portion. The secretions from the inner tier are thicker than from the middle tier, and in cross-sections appear roughly triangular in shape (Fig. 2 *F*). There were no nerve fibers observed for the outer tier, and it differs in this respect from the two inner tiers. In certain cases, after tapping, the outer cells unfolded, as it were, and spread out into a band. The distal ends are rounded, while the proximal ends are drawn down into a point which extends between the distal ends of the middle tier. Thus the nuclei of the middle tier are found between these points of the outer tier (Fig. 1 *A*).

The series of cross-sections (Fig. 2 *A*–*F*) are taken at the levels of the different nuclei.

I. The first section beneath the cornea is shown in Fig. 2 *A*. It represents the extreme distal portion of the ommatidia. A few large nuclei are found at this level, situated between the individual ommatidia.

II. The next figure (Fig. 2 *B*) is taken through the nuclei of the outer tier of cells, two sections intervening between *A* and *B*. These nuclei differ in shape from the round ones of the middle tier.

III. The next section (Fig. 2 *C*) shows two sets of nuclei, the larger ones (*n*) belonging to the middle tier of cells, the smaller (*p*) being the nuclei from the surrounding pigment cells (Fig. 1 *A*, *p*).

IV. Fig. 2 *D* shows a section through the nuclei of the middle tier of cells. This drawing is from the same section as *C*, but drawn at a lower level.

V. The following figure (*E*) is the fourth section after *D*. The round nuclei are from the clear cells or supplementary cells.

VI. Situated at about the same level as the nuclei shown in Fig. 2 *E*, but in the next section (Fig. 2 *F*), are the nuclei belonging to the inner tier of cells (Fig. 1 *A*, t_3).

The nuclei shown in Fig. 2 *E* belong to a group of cells lying between the two proximal tiers of cells. These cells are very different from any of the others found. They are colorless and contain no granules. Fig. 1 *D* shows two cells from the middle tier, between them one of these supplementary cells, in its natural position. The supplementary cells are extremely delicate, sending distally a fine process between the cells of the middle tier, and proximally between those of the inner tier. The nucleus is small and easily distinguished from that of a cell of the inner tier. The nuclei are found at the level of the distal ends of the inner cells. There are four supplementary cells.

The crystalline body is surrounded by the tiers of cells described above. It is composed of segments — "Grenacher's segments." These segments are cone-shaped. At the level of the nuclei of the inner tier (Fig. 2 *F*) these are not seen in cross-section, the rhabdoms, only, belonging to these cells being visible. In maceration preparations they often separate from each other at the proximal ends, while found joined at the larger distal ends.

According to Adensamer there are nuclei in these bodies

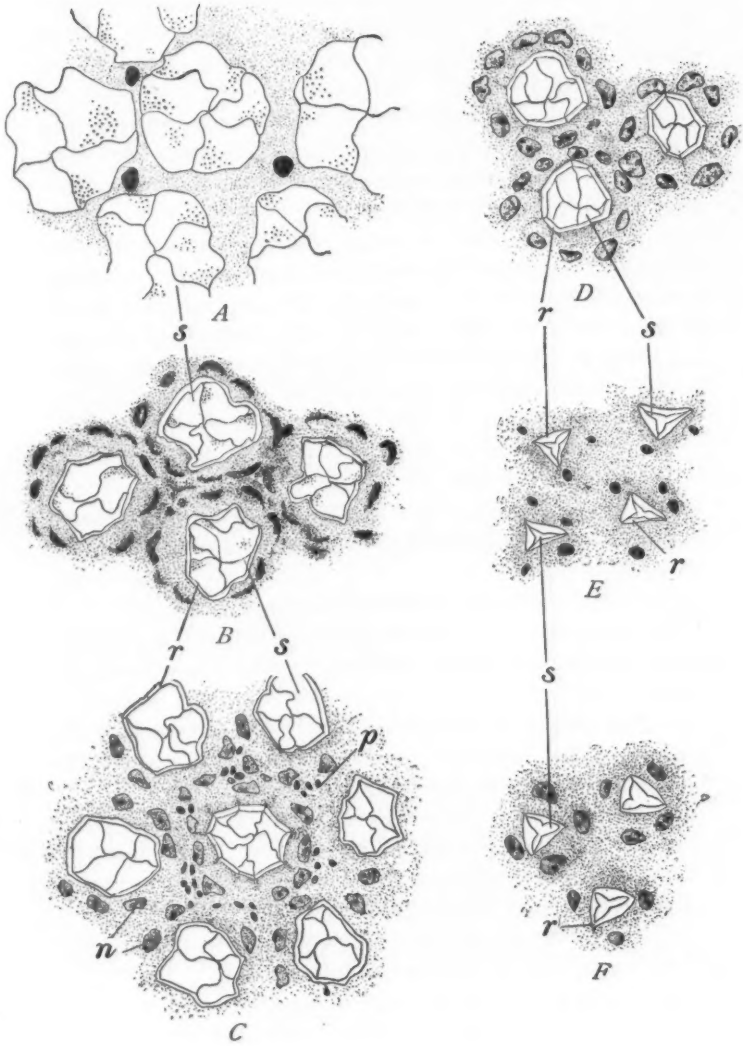

FIG. 2.

early in their existence, thus proving their cell nature. He also states that in an adult these can be vaguely seen. In no eye did I see an indication of nuclei in the segments of the crystalline body.

Cross-sections show the segments to be arranged in no regular manner. In a complete series of cross-sections one ommatidium was followed, and camera drawings at the high and low level were made of each section.

It was thus possible to trace each segment and find the number of segments and their relative position. In most ommatidia the number counted was ten to eleven, but in one ommatidium I was able to trace twelve. It must be understood that in a single section no more than six to eight appear. This can be seen by referring to Fig. 2.

Summary.

The species described by Grenacher is Scutigera (Cermatia araneoidea); by Adensamer, Scutigera coleoptrata; by myself, Cermatia forceps.

The latter is the only American Scutigera.

The differences in the accounts are probably to be explained in part by the fact that the individuals studied were of different species.

(1) The number of ommatidia in each eye of Scutigera forceps is about two hundred. In Cermatia araneoidea (Grenacher) the number is given as one hundred.

(2) The crystalline body was found to be made up of ten to twelve segments, instead of six to nine. No nuclei were observed in these segments.

Each ommatidium is made up of the following cells:

(3) Elongated pigment cells surrounding each ommatidium, sixteen to eighteen in number (p, Fig. 1 *A*).

(4) An outer tier of pigment cells, embracing the distal portion of the crystalline cone, ten to twelve in number (t_1, Fig. 1 *A*).

(5) A middle tier of cells of ten to twelve (t_2, Fig. 1 *A*).

(6) An inner tier of cells situated at the proximal end of the

ommatidium, touching with their proximal ends the basal membrane. In the inner tier there are from three to four cells (t_3, Fig. 1 *A*).

The cells of (5) and (6) secrete, upon their inner surfaces, rhabdoms, and from the outer side send out a process constituting the nerve fibers.

These nerve fibers were mentioned by Adensamer, but his figures failed to show the direct connection between the fibers and the cells of the middle and inner tiers.

In macerated preparations I have been able to show this beyond doubt (Fig. 1 *C*, *D*), and in the ommatidium, before it has been separated into its component parts, have observed the passage of these fibers through the basal membrane.

The expanded proximal portions of the elongated pigment cells (Fig. 1 *B*, *p*) form the layer of pigment spoken of by Adensamer, as found on the basal membrane.

(7) Supplementary cells, four in number, are found at the same level as the cells of the inner tier. They are entirely different, and thus easily distinguished from the cells of the inner tier (*a*, Fig. 1 *D*).

(8) As shown in Fig. 2 *A* certain large nuclei were found in cross-sections at the distal part of the ommatidium. They are found only in the space between three ommatidia. They were not observed, nor the cells to which they belong, in maceration preparations.

BRYN MAWR COLLEGE, April, 1900.

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